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THE ASSUMPTION OF ADAPTIVITY IN GENITAL MORPHOLOGY

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The "Lock And Key" Hypothesis, first proposed by Dufour (1844), holds that the morphology of insect genitalia is an adaptive character which serves as a prezygotic reproductive isolating mechanism. This popular notion has long been used as a rationalization of the emphasis on genital morphology in taxonomic work, even though a functional explanation of a character's biological significance is not a necessary condition for its use in classification. The hypothesis was widely supported in the literature in the 1940s in the heyday of the "New Systematics," when there was tremendous interest in reproductive isolating mechanisms in general, and it found a place in such classic evolutionary syntheses as Dobzhansky (1951) and Mayr (1963). As Mayr noted, however, genital incompatibility would come into play as an isolating mechanism only after the waste of time and energy in courtship; thus it would tend to be superseded by other (behavioral, pheromonal) mechanisms which would act at an earlier stage. Rentz (1972) recently demonstrated that mechanical isolation can be an effective barrier to hybridization in katydids (Orthoptera: Tettigoniidae). However, other (ecological) factors comonly prevent interspecific courtships in nature.

The attitude of Lepidoptera taxonomists has been largely shaped by Klots (1933), who wrote in his landmark revision of the Pieridae that "changes in the genitalia must of necessity be . . . slowly effected . . . a change in the structures of one sex can only survive if there are corresponding changes in the structures of the other." Moreover, "The development of practically all of the external features . . . must be regarded as modifications to some degree controlled by the physical environment of the species. The development of the genitalia must be regarded as . . . nearly or entirely independent of such environment." These are powerful, deductive arguments for the conservatism of the

genitalia, making them a very desirable and heavily weighted character in conventional taxonomy. However, a series of relatively little-known studies carried out in Germany casts Klots' arguments into very serious doubt, and with them the "lock and key" hypothesis as well.

H. J. Müller has carefully studied the phenotypic plasticity of the leafhopper genus *Euscelis* (Homoptera: Ciccadellidae). The "morphospecies" *E. plebeius* and *E. incisus,* which are "good species" by the conventional criteria of the "dead-bug taxonomist," were shown to be photoperiodically induced seasonal phenotypes of one species, and either could be produced from a brood of the other by environmental manipulation alone (Müller, 1954, 1957, 1961, 1965). This is hardly the first time biological information has overthrown a classification based solely on morphology, but it is of special interest because the genitalia were specifically at issue, and Müller was able to demonstrate that their morphology was in fact under photoperiodic control. In fact, aedeagus width, hitherto used as a taxonomic character in *Euscelis,* was shown to be an extremely sensitive index of developmental daylength (Müller, 1957). The dogma that the genitalia are insulated from environmental influences can no longer be sustained. Again, this is not terribly surprising: the developmental processes giving rise to various structures of an organism have to be coordinated in some way, even though some are more buffered against the external environment than others. More intriguing is Müller's determination that growth rate, and the durations of the nymphal instars, are independent of daylength. This implies that specific developmental processes are under photoperiodic control, and that seasonal disparities in genital morphology are not simply consequences of differences in growth rate. But are the genital variants somehow adaptive? If *E. plebeius* and *E. incisus* were good species as previously thought, they would be thought to be reproductively isolated by their differences. Does it make biological sense for the seasonal generations of a single multivoltine species to be isolated from one another?

Fortunately the problem has been solved. *Euscelis* was the subject of the most thorough study of the functional anatomy of insect genitalia ever published (Kunze, 1959). By studying pairs preserved *in copula,* Kunze was able to describe in minute detail how the parts of the male and female genitalia function in copulation, and how this function is affected by seasonal changes. A

few quotes from Kunze highlight those findings which are relevant to the "lock and key" hypothesis.

> Only a loose morphological correlation exists between the male and female reproductive organs, albeit these organs do bear species-specific characteristics. A narrow, shape-determined correspondence, such as that between a complicated lock and its key, was not demonstrable. (p. 384)
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> As anatomical study demonstrated, spring and summer generations of *Euscelis plebeius* differ considerably in the form and width of the penile shaft; they are largely similar, on the other hand, with respect to the formation and size of the female genital space. It follows . . . that the dimensions of the male and female copulatory organs . . . can vary within certain limits without reducing their functional capacity. This inference . . . may be confirmed relatively easily through mating of different seasonal forms, since spring and summer forms can be reared simultaneously, and differential copulatory behavior of the two forms was not observable.
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> Supposing it to be the case that the morphological correspondence between the penis and the female genital space were as precise as that between a key and its appropriate lock, a successful copulation between different seasonal forms would be impossible, or at least greatly hampered. (Müller) carried out appropriate mating attempts between the two seasonal forms . . . the results of which he published in 1957. I have carried out similar tests . . . in order to control for the correctness of the anatomical data. . . . The findings confirm Muller's results. From them the following conclusion must be drawn: the shape of the penis in *Euscelis plebius* is not linked to its function in every detail; rather it can vary in rather large measure, without impairing successful copulation. (pp. 360-361)

Since the genitalia are so widely used in Lepidopteran taxonomy it is worth noting that Reinhardt (1969) has found morphological differences in the genitalia of the photoperiodically-induced seasonal forms of the common Palaearctic Nymphalid *Araschnia levana.*

In summary, the following points deserve consideration before blind assumptions are made regarding the function and taxonomic value of genital characters:

1. The assumption that interspecific differences in genital morphology function as a prezygotic reproductive isolating mechanism is unwarranted unless actual experimental or field evidence of inability to mate can be produced, as in Rentz's tettigoniid work, or the differences are of such a gross nature that copulation is unquestionably impossible.

2. Even if satisfactory evidence according to the criteria in (1) is forthcoming, this does not mean the genitalic difference is a

regular functional isolating mechanism in nature, let alone the only one. In most cases, close study demonstrates ecological or behavioral isolating mechanisms which keep the species apart long before attempted copulation.

3. Although the genitalia may be more conservative in time than many "superficial" characters, they are not insulated from environmental influences and may vary seasonally or otherwise as a consequence of direct developmental control or allometric processes. The *Euscelis* case demonstrates that without sophisticated knowledge of the functional anatomy of the genitalia of both sexes, the potential for reproductive isolation may be grossly misjudged, and erroneous taxonomic decisions may result.

4. Even in the absence of seasonal differences, large samples commonly reveal variability in genital characters which is comparable to that observed in "superficial" ones. With small samples, this variability may be incorrectly taken to have taxonomic significance. Descriptions of new taxa should whenever possible base genitalic data on more than a single preparation. This is of course merely good taxonomic practice and a deliberate avoidance of typology.

Butterfly taxonomy is undergoing a wave of splitting, a periodic phenomenon likely to be with us for a while. New taxa have been described in several groups, particularly the Lycaenidae, based on questionable genitalic characters. If biological data cannot be obtained it is incumbent on the taxonomist to continue to behave as if the biological species concept, and all the "population thinking" that goes with it, still applies. The dogma of the "lock and key" is dangerously typological.

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